PATTERNS OF LARVAL DEVELOPMENT IN STENOGLOSSAN GASTROPODS

GEORGE E. RADWIN AND J. LOCKWOOD CHAMBERLIN

ABSTRACT.—Studies of egg capsules and the mode of development in certain species of stenoglossan prosobranchs from the northeastern Gulf of Mexico revealed an apparent disproportionate number of species with non-pelagic larval development. Thorson (1950) suggested that among shallow-water marine invertebrates incidence of pelagic development increased from the arctic to the tropics and predominated in the subtropics and tropics. His conclusions were based largely on prosobranch mollusks. We suggest that the mode of early development in the Stenoglossa tends to follow phyletic lines, regardless of latitude or climatic conditions.

Many prosobranch gastropods lay their eggs in parchment-like capsules, separately or in clusters, attached to firm substrata. Unequivocal species identification is possible when the capsules are deposited in an aquarium containing individuals of a single species or when observations on ovipositing snails are made. The young of most higher prosobranchs pass the veliger stage within the capsule and may be sufficiently developed before emergence to be identifiable either by the sculpture of the early teloconch sculpture or by the radular dentition. In other groups the young are released as veligers and are carried in the plankton until they settle and metamorphose. Pearse (1969) described a third mode of development which seems to be intermediate between these two. In this type a modified veliger (called by some authors a veliconcha) emerges from the egg capsule and swims feebly for a short time in the bottom-most layer of water before settling. He has called this a demersal mode of development. The only stenoglossan species we know to exhibit this kind of development is *Olivella verreauxi* (Duclos).

Identification of capsules of marine gastropod species can contribute to distributional data which may be useful in zoogeographic studies and may serve as an ecological tool in determining the reproductive range of a species. In addition, their use as taxonomic characters at the generic level should be considered.

In this paper the spawning conditions and egg capsules of nine species of stenoglossan mollusks from the northeastern Gulf of Mexico are described. These observations were made from March 1963 to July 1964. The species treated are: *Phyllonotus pomum* (Gmelin), *Muricanthus fulvescens* (Sowerby), *Calotrophon ostrearum* (Conrad), *Urosalpinx tampaensis* (Conrad), *Urosalpinx perrugata* (Conrad), *Thais floridana* (Conrad), *Cantharus cancellarius* (Conrad), *Cantharus multangulus* (Philippi), and *Pollia tincta* (Conrad).

SPAWNING SITES, EGG CAPSULES, AND LARVAL DEVELOPMENT

Phyllonotus pomum (Gmelin, 1791) (Fig. 1, 1a). Localities: St. Teresa and Bay Mouth Bar, Franklin Co., Fla., attached to large, empty bivalve shells. Period: May-July. The capsules are deposited in irregular compact masses up to 30 cm across; individual capsules are superficially similar to those of *Buccinum* and *Neptunea*. From two to five larvae develop in each.

Tryon (1880), Webb (1942), and Perry and Schwengel (1955) described and figured the capsule mass of *P. pomum*, and Webb reported communal spawning by as many as twenty-five females. This egg mass is similar to that reported for *Murex senegalensis* (see Knudsen, 1950). D'Asaro (1970b) reported non-pelagic development for *P. pomum*.

Muricanthus fulvescens (Sowerby, 1834) (Fig. 5). Locality: St. Andrews State Park, Bay Co., Fla., attached to rocks of the breakwater. Period: June-August. Capsules deposited in clusters with their bases fused. Each capsule is a flattened cylinder about 25 mm

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high, with the top broader than the base. All were empty when collected. Identification was made on the basis of a laying female and an egg mass (catalogue no. 599643) in the collection of the Division of Mollusks, U.S. National Museum of Natural History. Moore (1961: 26) figured a similar capsule collected off Mississippi as *M. fulvescens*. He gave the height of "one typical specimen" as 14 mm which, from the examples we have seen, seems to be too small. He also reported that there are over one hundred eggs in each capsule.

Calotrophon ostrearum (Conrad, 1846) (Fig. 7,7a). Localities: 1) St. Teresa, Franklin Co., Fla., on the blades of turtle grass; 2) dredged in 13 m off Dog Island, Franklin Co., Fla., attached to the sides of egg capsules of *Ficus communis* (Röding); and 3) attached to the walls of aquaria in which specimens of *C. ostrearum* were isolated (see Radwin and Wells, 1968). Period: early May to mid-June. Numerous capsules are laid individually, their bases separated; they are roughly semicircular, average about 4 mm high, and when first deposited usually contain 3 to 5 large, spherical, reddish eggs. Emergence is in the crawling stage (pelagic stage absent). Egg capsules apparently of this species were attributed by Perry and Schwengel (1955) to both *Urosalpinx perrugata* and *Cantharus floridanus*.

Urosalpinx perrugata (Conrad, 1846) (Fig. 2). Localities: 1) Bay Mouth Bar, Alligator Harbor, Franklin Co., Fla., attached to empty mollusk shells; 2) attached to the sides and bottoms of aquaria in which adults were isolated (see Radwin and Wells, 1968). Period: late April to mid-June. Numerous erect capsules, with fused bases, are deposited in a mat; the capsules, about 10 mm high, are inversely pyramidal and have two lateral alae and apical protuberances. An egg mass may contain as many as 200 capsules. A large but undetermined number of eggs is initially deposited; the majority are apparently nurse-eggs, since only 5 to 15 larvae develop fully. Larvae emerge in the crawling stage (pelagic stage absent). Egg capsules of this species are misidentified in Perry and Schwengel (1955) as the product of *Nassarius vibex*.

Urosalpinx tampaensis (Conrad, 1846) (Fig. 3). Locality: Attached to the floor of an aquarium in which individuals of this species were isolated (see Radwin and Wells, 1968). Period: March (in aquarium). The erect egg capsules, about 8 mm high, are deposited singly. They resemble plump fingers on stalks and are more similar to those of *Eupleura sulcidentata* (see Perry and Schwengel, 1955) than to those of the other two western Atlantic species of *Urosalpinx* (*cinerea* and *perrugata*). Each capsule contains numerous eggs which, in our material, did not develop.

Thais floridana (Conrad, 1837) (Fig. 4,4a). (For characters distinguishing this species from *T. haemastoma*, see Radwin and Wells, 1968.) Locality: St. Andrews State Park, Bay Co., Fla., attached to empty bivalve shells and rocks of the breakwater. Period: July-August. The elongate, trough-shaped capsules are about 12 mm high, have apical escape pores, and are deposited in large masses. The capsules at the base of a mass tend to be nearly erect and are attached side by side to the substratum, with their bases fused. Other capsules are attached to those beneath in an arborescent pattern.

Burkenroad (1931) figured a capsule mass and commented on the hatching process. D'Asaro (1966), who figured the capsule and described the spawning and embryology in detail, reported communal spawning occurring from February through November at Miami, Fla. He suggested that spawning "probably occurs also in December and January when the temperature is above average." A shorter spawning season in the northeastern Gulf of Mexico is consistent with the shorter period of warm water temperature there. Large numbers of veligers emerge and have a prolonged pelagic development (D'Asaro, 1966). This mode of development (also reported by other workers for this species in North American waters) contrasts with that of most stenoglossans treated in this paper.

Thorson (1946, 1950) cited *T. floridana* as having pelagic development in some parts of its range and direct, non-pelagic development in others. This may be correct, but his evidence is apparently inferred from Lamy (1928), who referred, in turn, to Korschelt and Heider (1900), which reference we have not seen. Lamy reported only that many of the larvae die after cleavage and are then eaten by the others in the capsule. Although this "nurse-egg" type of feeding is usually associated with non-pelagic larval development, it

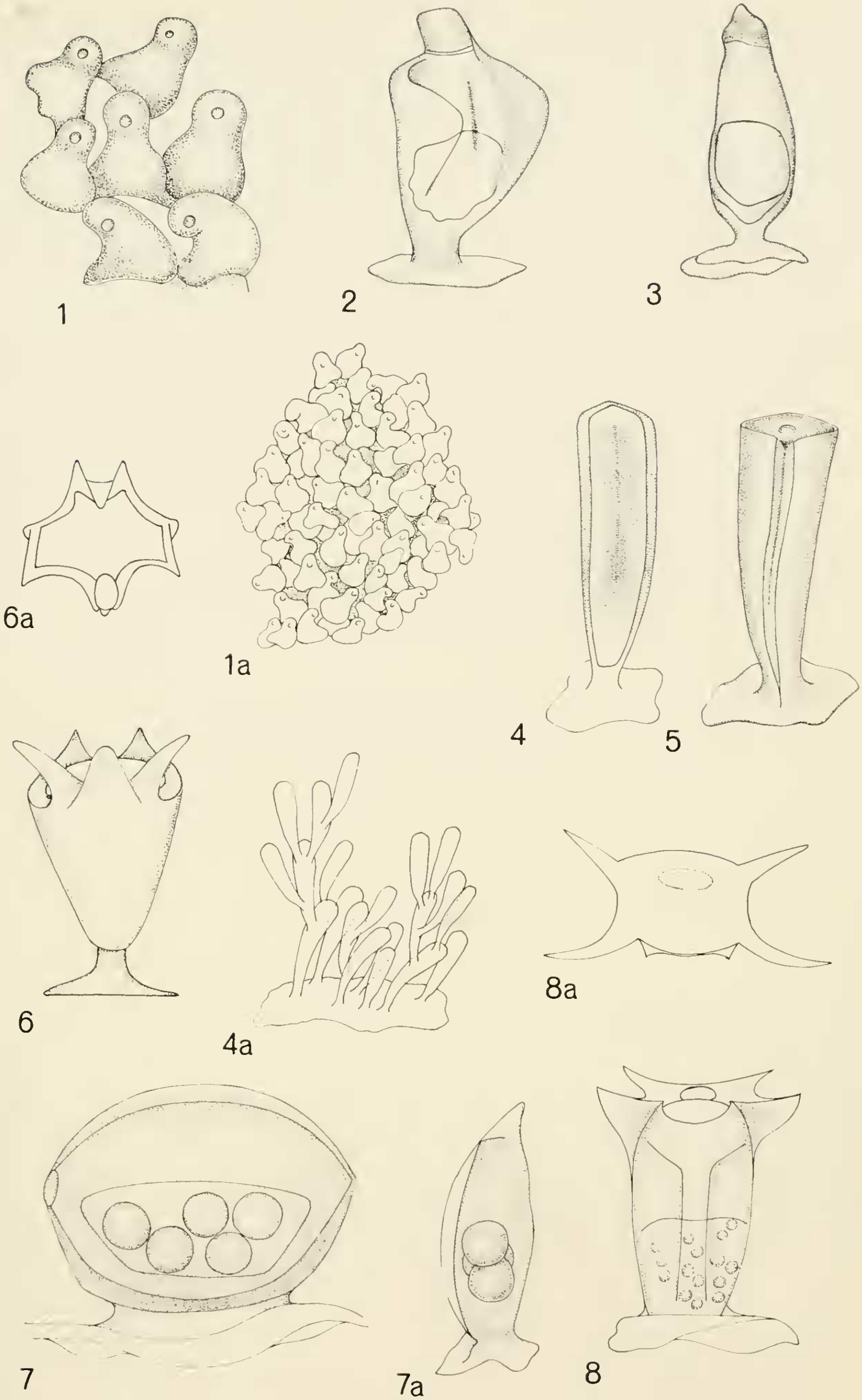

Figure 1. *Phyllonotus pomum*—seven capsules from an egg mass. 1a, *P. pomum*—small egg mass. 2, *Urosalpinx perrugata*—single egg capsule. 3, *Urosalpinx tampaensis*—single egg capsule. 4, *Thais floridana*—single egg capsule. 4a, *Thais floridana*—portion of an egg mass. 5, *Muricanthus fulvescens*—single egg capsule. 6, *Cantharus multangulus*—single egg capsule. 6a, *Cantharus multangulus*—top view of a single egg capsule. 7, *Calotrophon ostrearum*—single egg capsule. 7a, *Calotrophon ostrearum*—side view of a single egg capsule. 8, *Cantharus cancellarius*—single egg capsule. 8a, *Cantharus cancellarius*—top view of a single egg capsule.

is not proof of such development, as Thorson (1950) pointed out for *Natica catena.*

Cantharus cancellarius (Conrad, 1846) (Fig. 8, 8a). Localities: 1) Bay Mouth Bar, Alligator Harbor, Franklin Co., Fla., on empty mollusk shells; 2) Seahorse Key, Cedar Keys, Levy Co., Fla., on stones and empty mollusk shells; and 3) attached to the sides of aquaria in which adults were isolated (Radwin and Wells, 1968). Period: early May to late June. The erect capsules are deposited in a mat with their bases confluent. In nature the mats contained 15-20 capsules; the number of capsules laid in aquaria was smaller. Individual capsules are roughly rectangular, have four distinctive spinose projections at the top, and are about 4 mm high. In each capsule approximately 10-20 larvae develop to the crawling stage.

Moore (1961:26) figured a capsule of this species as *Cantharus reticulatus.* He also noted that on the Mississippi coast "these capsules are rather common objects during March, April, and May," and that from one capsule "a dozen or more eggs hatch out while still in the veliger stage." We have seen no other report of pelagic development in this species or elsewhere in the entire family Buccinidae.

Cantharus multangulus (Philippi, 1849) (Fig. 6, 6a). Capsules illustrated in Perry and Schwengel (1955), fig. 340. Localities: 1) Bay Mouth Bar, Alligator Harbor, Franklin Co., Fla.; 2) St. Teresa, Franklin Co., Fla.; and 3) deposited on the floor of aquaria. The capsules collected in the field were on shells and turtle grass. Period: May-July. Each capsule is inversely pyramidal and about 4 mm high; the top surface bears four spine-like projections. The capsule mass is a mat formed by the confluent bases of the capsules. When first deposited each capsule contains 8-20 flesh-colored eggs, a number of which apparently serve as nurse-eggs, as only a few crawling-stage larvae eventually emerge from each capsule.

Pollia tincta (Conrad, 1846) (see Perry and Schwengel, 1955; Lebour, 1945). Localities: St. Teresa, Franklin Co., Fla., and Seahorse Key, Cedar Keys, Levy Co., Fla., on shells and small rocks. Period: June-July. Clusters of several capsules are deposited, each about 5 mm high, broadly goblet-shaped and basally pedunculate. Each capsule contains 5 to 15 eggs, which, in our material, did not hatch. Lebour (1945) described the larval development as non-pelagic. Generic distinction of *Cantharus* and *Pollia* (as *Pisania*), based on radular dentition (see Troschel, 1866), is corroborated by differences in egg capsule morphology. *Cantharus* capsules are four-sided and rectangular or inversely pyramidal, with a flat top. *Pollia* capsules are goblet-shaped.

DISCUSSION

The nine species studied belong in either the family Muricidae (six species) or the Buccinidae (three species), and constitute a majority of these families reported to live in the area of field work (Perry and Schwengel, 1955). The two families are both in the suborder Stenoglossa, order Neogastropoda.

Among shallow-water, benthic, marine invertebrates, Thorson (1950) found that species with pelagic larval stages were rare in polar regions but increased, and indeed predominated toward the tropics. This conclusion was based primarily on samples of prosobranch mollusks from several widely separated areas. However, our data and those of D'Asaro (1970) indicate that at least in the stenoglossans, non-pelagic forms of development may be more common in tropical waters than is generally recognized. Thorson's data demonstrate a substantial increase in the percentage of species with pelagic development from arctic to temperate waters (0% in East Greenland to 63.5% in southern England) but they show a much smaller increase in percentage from temperate to tropical waters (e.g. southern England to a) Canary Islands, 4.5%; b) Persian Gulf, 11.5%; c) Bermuda, 21.5%). These facts have led us to question whether the proportional increase implied by Thorson (1950) is demonstrable in lower latitudes.

A review of the literature on modes of larval development among marine prosobranchs shows that in the Archaeogastropoda there is no clear predominance of either pelagic or non-pelagic development. In the Mesogastropoda, however, pelagic development predominates. Within the Neogastropoda the suborder Toxoglossa exhibits pelagic larval development, whereas the suborder Stenoglossa is the only major prosobranch group in which non-pelagic larval development seems to clearly predominate (Table 1).

The apparent predominance of non-pelagic development in the Stenoglossa, regardless of latitude, as well as the abundance of species of this suborder in lower latitudes suggests that the Stenoglossa were under-represented in at least some of the areas discussed by Thorson. The Bermudas, the Canaries, and the Persian Gulf are not typical of the main tropical and subtropical shelf regions of the world. The first two are small island groups, separated from the adjacent mainland by deep water (over 1,000 m), and the third is a hypersaline body of water with excessively high water temperatures (Mohr, 1929) and a restricted outlet to the Indian Ocean.

Bermuda.—Lebour's (1945) data, on which Thorson (1950) based his estimate of 85% of Bermudan species having pelagic development, are biased toward species with pelagic development, as her study was based principally on plankton samples. Only 29 of her prosobranch species were sufficiently identified to be used in a calculation. Of these, only three (10%) are stenoglossans; two have non-pelagic development. All 26 of the non-stenoglossans have pelagic development.

The actual percentage of Bermudan prosobranchs with pelagic development, though apparently less than 85% may, nevertheless, be higher than is typical of tropical and subtropical western Atlantic areas. Evidence for this supposition stems from the fact that stenoglossans make up a smaller percentage of total prosobranchs at Bermuda than is typical of other similar areas. Peile (1927) listed 215 Bermudan species of marine prosobranchs, excluding abyssal species, of which 21% are stenoglossans. In comparison, faunal lists for the adjacent mainland and Caribbean island areas give the following percentages of stenoglossans: western Florida, 28% (Perry and Schwengel, 1955); West Indies, 29-32% (Arango, 1878; Dall and Simpson, 1901; Mörch, 1878); Brazil, 32% (Lange de Morretes, 1949).

Canary Islands.—Thorson (1950) reported that 68% of the Canary Islands marine prosobranchs exhibit pelagic development. Faunal lists for these islands and for the adjacent coast of western Africa indicate a situation parallel to that in Bermuda, with fewer stenoglossans among marine prosobranchs at the islands than at the mainland areas: Canaries, 30% (Dautzenberg, 1890, 1891); western Africa, 37% (Nicklés, 1950). São Thomé, in a more tropical position off the western coast of Africa, has an essentially similar situation; 28% of the marine prosobranchs are stenoglossan (Tomlin and Shakleford, 1923).

Evidence of a lower percentage of prosobranchs with non-pelagic larval development at Bermuda, the Canaries, and São Thomé is, in itself, of biogeographical and ecological interest. The faunal lists cited above show that the marine mollusks of these islands include few endemics. Such low endemism is evidence of recent faunal origin by immigration. The marine molluscan fauna of Bermuda is considered a depauperate Antillean fauna (Warmke and Abbott, 1961), and the prosobranchs of the Canaries and São Thomé are just as clearly depauperate western African. The colonization of these islands largely by species with pelagic larvae could be attributed to their ability, as larvae, to traverse the geographical and bathymetric barriers isolating the islands from the mainland.

Persian Gulf.—Thorson (1940a, 1950) found that 75% of the prosobranch species studied from the Persian Gulf had pelagic development. His data seems moderately biased toward such species as only 24% of them (5 of 21 species) were stenoglossans. Melvill and Standen (1901) and Melvill (1928) indicate that just over 30% of the marine prosobranchs from this area are stenoglossans.

In view of Thorson's original data showing only a small increase in the percentages of prosobranch species with pelagic larval development from temperate to tropical waters the question arises whether any significant increase exists. Regardless of the answer to this question—and our evidence is not enough to resolve it—there remains the question of why a steep gradient exists in higher latitudes but only a weak one (if, indeed, any exists) in lower latitudes. Of course, data on larval ecology and distribution must include other invertebrate groups as well.

After a draft of this paper was sent to Thorson in 1968, he informed us (in litt.) that the data he had compiled on stenoglossan early development, more extensive than the data in Table I, suggest an appreciably lower percentage of species with non-pelagic de-

TABLE I
OCCURRENCE OF PELAGIC AND NON-PELAGIC LARVAL DEVELOPMENT WITHIN THE STENOGLOSSA

Omit

Superfamily Family Genus	No. Species With Pelagic Larvae	No. Species With Non-pelagic Larvae	Reference
Muricacea			
Rapanidae			
Rapana	3	—	18,37,83
Muricidae			
Murex	4	5	15,43,63,75,83
Chicoreus	—	3	26,62,76
Phyllonotus	3	1	26,83
Boreotrophon	—	6	30,50,55,85
Calotrophon	—	1	xx
Bedevina	1	—	61
Bedeva	—	1	7
Favartia	—	1	74
Vitularia	1	—	25
Ceratostoma	—	1	6
Ocenebra	—	1	30
Urosalpinx	—	3	11,34,xx
Eupleura	—	1	11
Thaididae			
Purpura	1	—	49
Neptunea	—	4	6,30,40
Siphonalia	—	1	81
Pollia	—	1	48
"Cantharus"	—	2	xx
Buccinum	—	8	30,84
Volutharpa	—	1	30
Macron	—	1	14
Chauvetia	—	1	30
Melongenidae			
Melongena	—	1	35,45,71
Syrinx	—	1	36,61
Busycon	—	3	45,71,xx
Hemifusus	—	1	6
Fasciolariidae			
Leucozonia	—	2	26,49,75
Peristernia	—	1	x
Fasciolaria	—	3	26,45,xx
Pleuroploca	—	2	45.75
Fusinus	—	2	6,14,43
Troschelia	—	1	30
Volutacea			
Volutidae			
Voluta	—	2	45,80
Thais	9	1	6,15,24,26,43,45,49,63,83
Nucella	—	3	30,39,47
Buccinacea			
Columbellidae			
Pyrene	—	2	72
Mitrella	1	1	6,63
Anachis	5	1	6,25,54,78
Zafrona	1	—	4,6
Astyris	—	1	82,85
Amphissa	1	—	70
Columbella	2	1	43,72
Nassariidae			
Nassarius	11	3	3,17,30,41,42,45,63,79,83,92,93
Tritia	2	2	3,5
Ilyanassa	1	—	79
Buccinidae			
Beringius (Jumala)	—	4	21,30,50,82
Volutopsius	—	1	30,85
Pyrulofusus	—	2	22,32
Colus	—	9	30,82,84,xx
Plicifusus	—	1	50
Alcithoe	—	1	33
Melo	—	3	6,20,38,88
Cymba	—	1	51
Cymbiola	—	2	9,45
Marginellidae			
Persicula	—	1	43
Marginella	—	7	43
Prunum	—	1	26
Cancellariidae			
Cancellaria	—	1	43
Admete	—	1	82
Vasidae			
Vasum	—	1	26
Mitridae			
Strigatella	3	—	26,66
Atrimitra	1	—	16
Turbinellidae			
Turbinella (Xancus)	—	1	26
Olividae			
Ancilla	—	1	63
Olivella	—	4	6,30,53,67
Oliva	1	—	65

x — E. Allison Kay, personal communication
xx — this paper

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Calotrophon	—	1	xx
Bedevina	1	—	61
Bedeva	—	1	7
Favartia	—	1	74
Vitularia	1	—	25
Ceratostoma	—	1	6
Ocenebra	—	1	30
Urosalpinx	—	3	11,34,xx
Eupleura	—	1	11
Thaididae			
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Cymbiola	—	2	9,45
Marginellidae			
Persicula	—	1	43
Marginella	—	7	43
Prunum	—	1	26
Cancellariidae			
Cancellaria	—	1	43
Admete		1	82
Vasidae			
Vasum	—	1	26
Mitridae			
Strigatella	3	—	26,66
Atrimitra	1	—	16
Turbinellidae			
Turbinella (Xancus)	—	1	26
Olividae			
Ancilla	—	1	63
Olivella	—	4	6,30,53,67
Oliva	1	—	65

x — E. Allison Kay, personal communication

velopment (62% compared to our 72%). Thorson's reasons for believing "that the species with a non-pelagic development predominate more in available data than they do in nature" are 1) these species have egg capsules which are large, conspicuous, and easy to discover; 2) they tend to be discovered more often with their capsules than do species with pelagic development because they have a longer spawning season; 3) the capsules are easier to identify to species and 4) his experience at the Canary Islands and in Thailand indicates "that most species with pelagic development there will reproduce in the hottest season of the year," whereas "biologists tend to make expeditions to such places at the cooler times of the year." Correction for these biases would lower Thorson's entire gradient of pelagic vs. non-pelagic development, except for the Arctic, where we have seen no evidence to indicate the existence of pelagic development among stenoglossans; thus the slope of the gradient probably would be increased from high to mid-latitudes. We would not, however, expect the slope to be changed much from mid- to low latitudes by corrections for any of the sources of bias suggested by Thorson, except his last one, which would, in theory, result in some steepening.

SELECTIVE ADVANTAGE OF NON-PELAGIC LARVAL DEVELOPMENT

The apparent predominance of non-pelagic development in the Stenoglossa has necessitated a more detailed review of early development in this group (Table 1). The mode of larval development in the Stenoglossa seems generally to follow phyletic lines, regardless of latitude or climatic conditions (beginning with the Buccinidae pelagic development is almost unknown). Exceptions include the Nassariidae, in which pelagic development is clearly predominant and the Mitridae, whose wide distribution in the Indo-west Pacific (Cernohorsky, 1965) suggests that the pelagic mode of development predominates. We cannot explain these apparent inconsistencies on the basis of our data.

Thorson (1950) argued that pelagic development is disadvantageous in the Arctic because the period of rich plankton production on which most pelagic larvae depend for food is too short. For the lower latitudes, where both modes of development are practical, the problem remains.

Garstang (1928) and Thorson (1950) showed that pelagic development permits rapid dispersal, repopulation of depleted areas, and establishment of dense populations when the larvae encounter optimal conditions. By contrast, non-pelagic larvae tend to remain in established optimal situations, are not as numerous as pelagic larvae, and are provided with protection and a large food supply by parental brooding. This mode inhibits rapid dispersal, repopulation of depleted areas, and short-term establishment of dense populations.

There is little information on the advantages of the various modes of larval development to marine prosobranchs and other marine invertebrates of shallow waters. Thus, the selective advantage of non-pelagic larval development in the stenoglossans is not clearly understood. However, most stenoglossans are carnivorous and, therefore, occupy relatively high trophic levels in their ecosystems. It seems reasonable to suggest that these animals are probably food-limited. Thus, it may be more advantageous for stenoglossans to use their energy in producing relatively few, non-pelagic young that can utilize "proved" local food resources, than to adopt the alternative strategy of producing vast numbers of highly vagile young that must find suitable conditions to insure survival.

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